The Bellerophont Controversy Revisited

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Abstract: An old controversy reestablished itself in the late 1970s and early 1980s that focused on the systematic placement of the enigmatic Bellerophontoidea (informally, "bellerophonts"), a group of planispirally coiled, wholly fossil molluscs. The controversy embraced three fundamental concepts that are based on different philosophical interpretations of shell form, muscle scar patterns, and other preserved shell features: 1) all bellerophonts were monoplacophorans; 2) all bellerophonts were gastropods; and 3) some bellerophonts were monoplacophorans and some were gastropods. A review of the main issues appearing in the literature since the early 1980s indicates that these three philosophical divisions still exist and, indeed, have become entrenched. An examination of the relevant anatomical and shell features of recent gastropods and monoplacophorans, and comparison with preserved features in enigmatic fossil forms, convinces us that the bellerophontoideans and the coiled and high-domed "monoplacophorans" (Cyclomya) were gastropods. Only the flattened, spoon- and cap-shaped monoplacophorans (Tergomya) were true monoplacophorans. We present a hypothetical scheme for the morphological diversification of gastropods from early monoplacophorans that could account for Cyclomya, Bellerophontoidea, Patellogastropoda, and Prosobranchia.

Key Words: Gastropoda, Monoplacophora, Bellerophontoidea, functional morphology, phylogeny

One of the more polarizing arguments in malacology in the latter half of the 20th century has been termed the "bellerophont controversy". At the heart of this controversy is the question of whether the Bellerophontoidea, an extinct group of bilaterally symmetrical univalved molluscs, of which *Bellerophon* Montfort (Fig. 1) is a typical example, were gastropods or monoplacophorans. If they were monoplacophorans, they were untorted and exogastric (with the shell coiled over the head). If they were gastropods, they were torted and endogastric (with the shell coiled over the foot as in the majority of extant gastropods). The history of the controversy has been summarized many times and need not be repeated here. Readers interested in exploring the details might begin with summaries published by Yochelson (1967 – an excellent introduction to the natural history and evolution of thought on the bellerophonts), Harper and Rollins (1982), Peel (1985b), and Wahlman (1992).

TERMINOLOGY

We use the term "bellerophont" in an informal sense to designate both the Bellerophontoidea and the coiled Cyclomya; that is, any planispirally coiled, univalved mollusc that definitely is not a cephalopod. We also use the term "monoplacophoran" in an informal sense because sev-

eral authors (Salvini-Plawen, 1980; Wingstrand, 1985; Peel, 1991; and Geyer, 1994) recently urged abandonment of that formal name. N. H. Ohdner (*In:* Wenz, 1940) introduced "Monoplacophora" with the intent that it would be an informal term separating the superfamily Tryblidioidea from the Polyplacophora. Knight (1952) formalized the name by including Monoplacophora as a gastropod order (Knight included the order Polyplacophora with the gastropods as well!). The fossil tryblidioids had long been considered patelliform gastropods with multiple muscle scars until Wenz hypothesized that they had been, in fact, untorted animals. The discovery of *Neopilina* Lemche (Lemche, 1957; also Lemche and Wingstrand, 1959) gave credence to that hypothesis.

Horný (1965a) established two new monoplacophoran subclasses, Tergomya and Cyclomya. Tergomya includes the cap-shaped or spoon-shaped monoplacophorans such as *Tryblidium* Lindström in which the plane of the muscle field lies outside the apical axis (a curved line marking the exact center of the shell during ontogeny) (Fig. 2A). Cyclomya includes a wide variety of coiled and uncoiled forms in which the plane of the muscle field intersects the apical axis (Fig. 2B). This appears to represent a distinct and natural morphological separation among shells exhibiting multiple pairs of muscle scars.
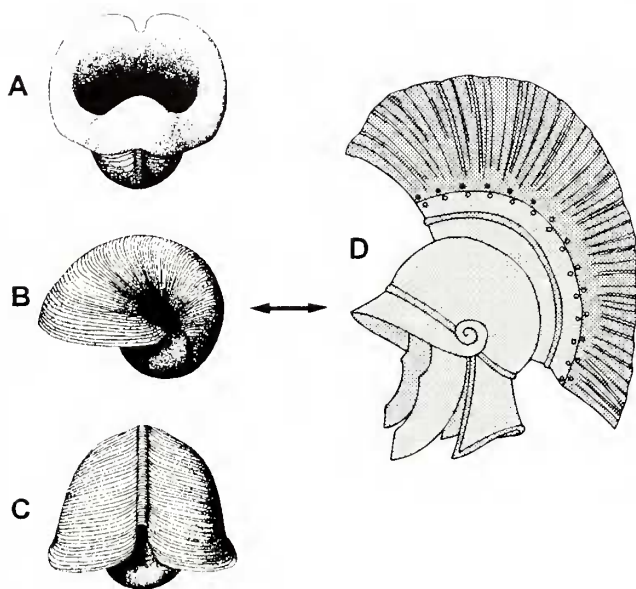
Fig. 1. *Bellerophon* Montfort, the isostrophically coiled mollusc that lent its name to the bellerophont controversy. **A** - Apertural view. **B** - Lateral view. **C** - Antero-dorsal view. Notice the similarity of the shell form to an ancient Greek helmet - **D**.

THE CONTROVERSY AND ITS EFFECTS

By the early 1980s many of those working with bellerophonts and/or molluscan phylogeny had encountered the puzzle of what to do with planispirally coiled, non-cephalopod, univalved molluscs bearing evidence of symmetrical, often multiple, muscles. As a result of quite different philosophies, these workers became polarized into three camps: group 1 – those who considered all bellerophonts to be monoplacophorans (Runnegar and Pojeta, 1974; Pojeta and Runnegar, 1976; Runnegar and Jell, 1976; Salvini-Plawen, 1980; Runnegar, 1981); group 2 – those who considered all bellerophonts to be gastropods (the majority of those who worked primarily on gastropod systematics and biostratigraphy); and group 3 – those who considered the bellerophonts a polyphyletic group that included both monoplacophorans and gastropods (Horný, 1963a, b, 1965a, b; Peel, 1972, 1974, 1976, 1980; Linsley, 1977, 1978a, b; Berg-Madsen and Peel, 1978). This third group considered that those bellerophonts having multiple sets of muscle scars were monoplacophorans whereas those with a single set of "columellar" scars were gastropods.

Harper and Rollins (1982) reviewed the controversy and critically examined the significance of shell structure, apertural re-entrants, parietal deposits, and muscle scars, all of which had been used at times by previous workers in distinguishing gastropods and monoplacophorans among the bellerophonts. All of these features have limitations in sys-

tematics, and at the time we felt muscle scars in particular were probably the least reliable single criterion on which to base a phylogeny. We concluded that placing bellerophonts and monoplacophorans in a single class based simply on shell form and muscle scar patterns was "tantamount to classifying bats, birds, and insects together because they all have bilateral symmetry and wings" (Harper and Rollins, 1982, p. 229).

Opinion in the paleontological community has changed little since the early 1980s. A review of the literature since mid-1982 indicates that group 1 still considers all bellerophonts to be monoplacophorans (Stanley, 1982; Runnegar, 1985; Runnegar and Pojeta, 1985; Signor, 1985; Geyer, 1994). Those in group 2 still consider the bellerophonts to be gastropods (McLean, 1984; Harper and Rollins, 1985; Kase and Nishida, 1986; Boucot *et al.*, 1986; Rohr and Yochelson, 1990; Frýda and Guitierrez-Marco, 1996; Ebbestad, 1999; and many others). Those in group 3 still consider the bellerophonts to be divided among the gastropods and monoplacophorans (Linsley and Peel, 1983; Peel, 1985a, b, 1993; Horný, 1986, 1993; Edlinger, 1988; Wahlman, 1992; Berg-Madsen and Peel, 1994).

The primary questionable contention that is driving the bellerophont controversy is that multiple pairs of symmetrical muscles in conjunction with the bilateral symmetry of the shell indicate a monoplacophoran affinity for all bellerophonts (Wenz, 1940; Runnegar and Jell, 1976; Salvini-Plawen, 1980; Geyer, 1994). This argument is based on the assumption that asymmetry is a necessary consequence of torsion, involving all internal and external organs, including the shell muscle. In effect, this argument ignores the innumerable biological investigations done over the past 200 years showing post-torsional symmetry of many gastropod species and their shell muscles, and even of organs such as the ctenidia, osphradia, and hypobranchial glands (as in many fissurelloideans). Yet the existence of multiple, symmetrical muscles has been used time and again as a valid systematic character allying such disparate molluscs as *Neopilina* Lemche and *Bellerophon* Montfort. For example, Rollins and Batten (1968), when confronted with conflicting morphological evidence, were persuaded to assign the sinus-bearing bellerophont *Sinuitopsis acutilira* (Hall) to the monoplacophorans based solely upon multiple symmetrical pairs of muscle scars.

TORSION AND ITS CONSEQUENCES

The argument that bellerophonts were untorted because asymmetry, as represented by helical coiling as well as asymmetry of soft parts, must be a necessary consequence of torsion has been reiterated by many authors (Ghiselin, 1966; Runnegar and Pojeta, 1974; Stanley, 1982;
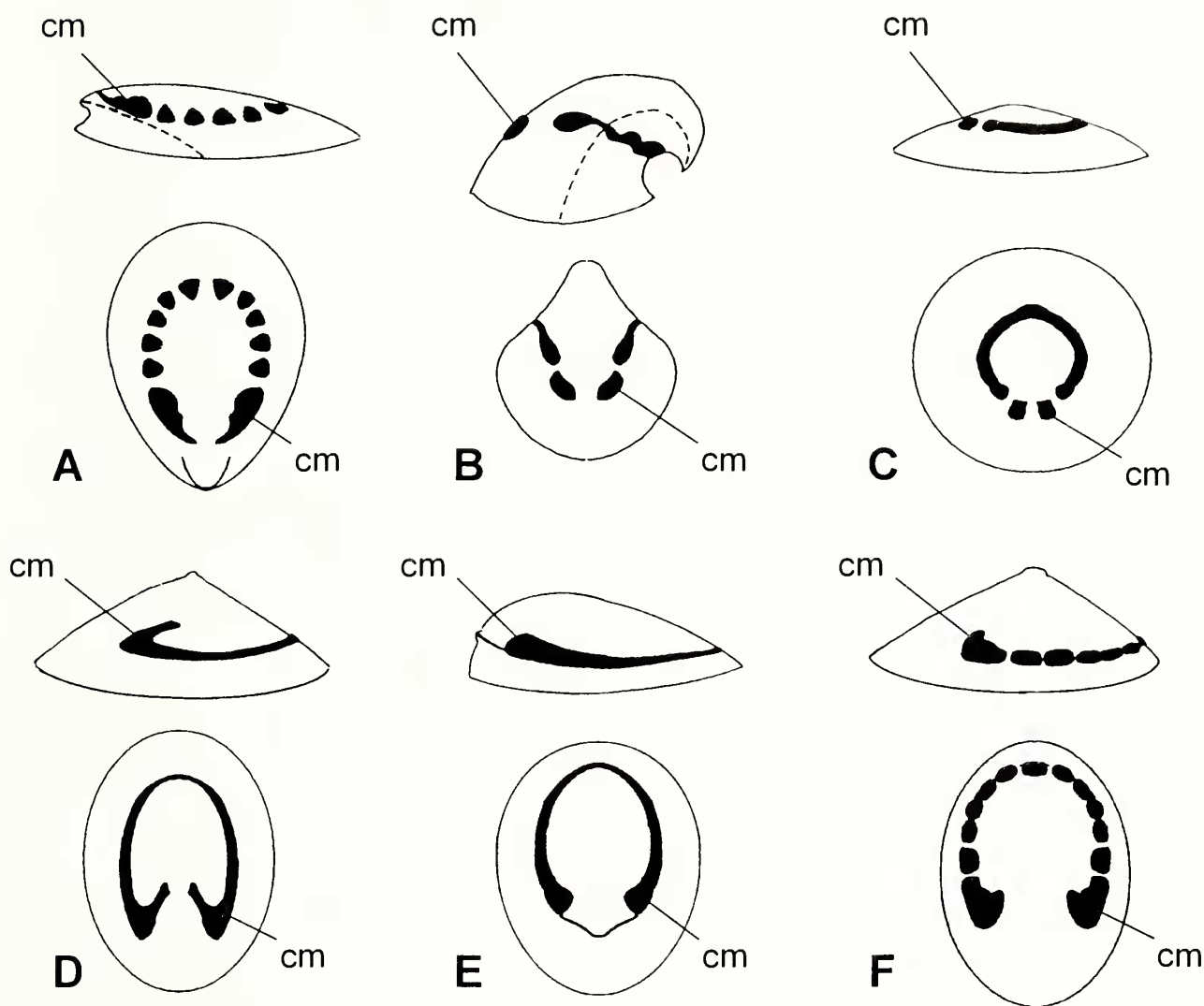
Fig. 2. Diagrams of representative tergomyan and cyclomyan monoplacophorans and patelliform gastropods, showing lateral and dorsal views of muscle scar patterns (black), including the discrete cephalic muscle (cm). **A** - Silurian tergomyan *Tryblidium* Lindström, showing the muscle field lying outside the apical axis (dashed line); **B** - Devonian cyclomyan *Cyrtonella* Hall, showing the muscle field intersecting the apical axis; **C** - Ordovician archinacelloidean *Floripatella* Yochelson; **D** - Recent fissurelloidean *Diodora* Gray; **E** - Recent acmaeoidean *Lottia* Gray; and **F** - Recent cocculinoidean *Cocculina* Dall.

Geyer, 1994, just to name a few). Linsley and Kier (1984), on the other hand, have argued that torsion and asymmetry are separate events in gastropod ontogeny; this has been shown to be the case by Bandel (1982). In fact, both the fossil record and the modern seas are full of prosobranch gastropods (torted) with symmetrical shells and opistho-branch gastropods and other molluscs (untorted) with heli-cally coiled shells. Haszprunar (1988a, b) also found no pri-mary correlation between torsion and helical coiling. He suggested that the occurrence of hyperstrophy in the proto-conchs of higher gastropods argues for two independent processes, demonstrating that the direction of shell coiling is not correlated with the direction of torsion. We therefore reject the notion that bellerophonts must be untorted because they were isostrophically coiled.

APERTURAL RE-ENTRANTS

One of the most frequently used shell features for separating gastropods from monoplacophorans are slits, sinuses, and other re-entrants on the margins of the shell aperture. For example, the Pleurotomarioidea are best-known for having a deep, narrow slit near the middle of the whorl that is used to channel the exhalant current away from the inhalant currents. Linsley's fourth "law" of

gastropod shell form states, simply, "Angulations or re-entrants on the aperture are usually indicative of inhalant or exhalant areas; inhalant areas will be directed as anteriorly as possible" (Linsley, 1977:200). This law makes sense only in motile animals – the gastropod has the advantage of sensing its environment in advance of its direction of motion. Because some bellerophonts have re-entrants situated laterally or postero-laterally, close to the shell coil, Starobogotov (1970), Berg-Madsen and Peel (1978), and others considered these forms monoplacophorans. However, Linsley (1977) admitted that he did not consider all gastropods when formulating this "law." Harper and Rollins (1982) argued that the fourth "law" was not necessarily applicable to limpets and other bottom clampers. Many limpet gastropods have "re-entrants" all around the shell, related to coarse radial ribs that end at the shell margin in small concave, v-shaped emarginations. Also, the inhalant and exhalant currents in limpets are not necessarily positioned anterior and posterior as they are in the helically coiled gastropods. In *Patina*, for example, the inhalant current enters the pallial groove along the length of the gill skirt and exits anteriorly through the right side of the nuchal cavity (Fretter and Graham, 1962). *Patella* similarly draws water in along the whole margin of the mantle, but expels it ventrally. In the caenogastropod limpet *Crepidula*, the current enters the mantle cavity on the left and leaves on the right – both inhalant and exhalant currents are lateral.

We agree that apertural reentrants should be a good indication of whether a mollusc is a monoplacophoran or a gastropod, but only if the animal is truly motile. However, of all the coiled "monoplacophorans" in which the muscle scars are known, none is what we would call a truly motile animal. We envision most of the cyclomyans as limpets or shell clampers (as opposed to those that retract the body into the shell like most prosobranchs). These forms commonly have large, tangential apertures and loosely coiled shells, as opposed to the tight coils and radial apertures of forms such as *Bellerophon*. They are also often covered with epibionts. This suggests to us that these forms were functionally limpet-like (although some very motile gastropods harbor shell-covering epibionts). The most functionally advantageous place for inhalant currents would be close to the gills and relatively far from the exhalant currents. As in *Patina*, *Patella*, and *Crepidula*, this could easily have been just about anywhere on the shell. We conclude that presence of lateral re-entrants is not a definitive criterion for separating limpet-like monoplacophorans and gastropods.

It should be noted that certain cyclomyans have small re-entrants on the aperture beneath the shell coil (*e. g. Neocyrtolites* Horný – see Horný, 1993, Pl. 1, Figs. 7, 8). If these functioned as inhalant currents, the animal almost certainly was exogastric. However, these features common-ly are very small and probably would not have been very effective for channeling currents into a large aperture. Their function is uncertain, but may have been associated with an operculum or some other feature.

COMPARISONS OF MUSCLE SCARS

The suggestion that multiple muscles are a hallmark only of the monoplacophorans has no basis in fact. Most non-helically coiled limpet gastropods (fissurelloideans, patellogastropods, cocculinoideans, etc.) have horseshoe-shaped muscle fields with a distinctive break at the anterior end that defines the position of the mantle cavity. In the Patellogastropoda, the muscle field appears to be continuous, but in fact it is arranged as a series of discrete muscle bundles separated by narrow clefts. In the Cocculinoidea the muscle bundles display a widely varying degree of separation (Haszprunar, 1987, 1988a). Thiem (1917) showed that the clefts allow space for afferent vessels to transfer blood from the foot and visceral mass into spaces in the mantle skirt where oxygenation takes place. The degree of separation appears to be directly related to the efficiency of the gills (Fretter and Graham, 1962). The Fissurelloidea have two very efficient ctenidia and no pallial gills, so the muscle bundles have little division (Fig. 2D). The Patellidae and Lottiidae exhibit well-developed pallial gills, and the Lottiidae have one ctenidium, so that oxygenation occurs easily. There are few afferent vessels and few muscle divisions (Fig. 2E). The Acmaeidae and Lepetidae have one ctenidium that is not very effective, and no pallial gills, so that pallial respiration via afferent vessels is necessary for adequate blood oxygenation. Species of these families commonly exhibit numerous muscle clefts. The separation of the individual muscle bundles is especially noticeable in the Cocculinoidea (Haszprunar, 1987, 1988a) (Fig. 2F).

Based on innervation of shell muscles in limpet gastropods, Haszprunar (1985) showed that there is only a single pair of muscles. However, he also indicated the possibility that a single pair of shell muscles divided into discrete bundles might be the primitive condition shared by monoplacophorans (Haszprunar, 1988b, p. 374).

It seems likely that multiplicity of muscles (regardless of division) is a normal condition in animals that pull the shell down to the substrate, as opposed to those that retract into their shells. It is also likely, based on those animals with discrete muscle bundles and those with seemingly solid horseshoe-shaped muscle masses, that environmental conditions and habitat diversity played a large part in the origination of the particular muscular condition. More muscle mass (the "solid" horseshoe) probably was an adaptation either to ward off predation or to the vagaries of near-shore conditions (storms, rough seas, desiccation

episodes, etc.). In either case, it would allow the animal to clamp the shell more tightly around the body and foot. If this is the case, then discrete, multiple muscles must indicate a lack of need, or less need, for such muscle mass. Indeed, modern monoplacophorans, which live in deep, quiet water, tend to have weakly developed muscles that leave no scars on their shell interiors. The Cocculinidae, which probably have the best set of discrete muscles among Recent limpet gastropods, also occur in deep water (McLean, 1987; Haszprunar, 1987). On the other hand, the fossil tryblidiids, which lived in shallow water and probably functioned in much the same fashion as modern limpet gastropods, had strong muscles inserted well into the shell.

The largest of the paired muscle bundles in modern limpet gastropods appears at the anterior end of the muscle field and is associated with retraction of the head. In at least two Recent limpet groups, Fissurelloidea and Lepetelloidea, this muscle pair has hook-like protrusions on the interior side of the bundle. McLean (1984) suggested these hook-like protrusions in the fissurelloideans mark the position of muscles that control the ctenidia. Although this is possible, we feel it is unlikely because similar hook-like protrusions occur on the cephalic muscles of many other limpets that have only one, or no, ctenidium. The Lepetelloidea, for example, have several pallial leaflets of secondary origin restricted to the right post-torsional side of the mantle skirt, outside the shell muscle field (Haszprunar, 1988b). The hook-shaped muscles also occur in Polyplacophora and in many Paleozoic monoplacophorans such as *Tryblidium* (cm in Fig. 2A). For McLean's hypothesis to be correct, the ctenidia in *Tryblidium* and other monoplacophorans would have to be situated in an anterior mantle cavity which, of course, does not exist in untorted molluscs. Alternatives include: 1) the hook-shaped muscles in fissurelloideans had distinctly different functions in monoplacophorans and, following torsion, the gastropod limpets adapted the muscle for use with the ctenidia; 2) the hook-shaped muscles are convergent features in the two lineages with no homologous functions; and 3) the hook-shaped muscles are homologous features but have a different function than suggested by McLean (1984). We prefer the third option, but are uncertain of their function. The hook-shaped muscles are likely related to retraction of the head and, possibly, anchoring of the buccal muscles. Purchon (1977, p. 467), in discussing the muscles of Recent monoplacophorans, described a "complex series of muscles inserted into the shell anteriorly on either side of the mouth [that] serve to move the lips of the mouth, the velar lobes, the post-oral tentacles, and the radular apparatus." Although the cephalic muscle area of *Neopilina* Lemche does not look much like that of *Tryblidium* Lindström, in all likelihood they are homologous, as well as analogous, structures. It may be that the change from a shallow water, presumably

herbivorous mode of life in Paleozoic monoplacophorans to a deep water, deposit feeding mode of life in Recent forms accounts for the differences.

We should, therefore, be able to use the relatively larger cephalic muscles in cap-shaped or spoon-shaped monoplacophoran and gastropod limpets to recognize the anterior ends of the shells. In *Tryblidium* Lemche (Fig. 2A) the cephalic muscles occur near the shell apex, indicating the animal's exogastric nature. In the gastropod limpets (Figs. 2C-F) the cephalic muscles should occur on the end opposite the shell apex (endogastric). The same is true of the archinacelloideans (Fig. 2C) which, despite their apparent tergomyan appearance, generally are considered to be gastropods (Starobogotov, 1970; Harper and Rollins, 1982; Yochelson, 1988; Mazaev, 1998). (Note, however, that in many limpet gastropods, the "coil" is anterior or centralized. Therefore, the terms "endogastric" and "exogastric" are essentially meaningless without reference to soft anatomy.)

We suggest these cephalic muscles also occur in the cyclomyans as the pair of subcircular to oblong muscle scars on the shell dorsum, farthest from the shell coil (Figs. 2B, 3A). Dzik (1981) reconstructed the cyclomyan *Sinuitopsis* Perner with these muscles acting as retractors for an operculum on the trailing foot of the animal. We find this highly unlikely, not because there is no evidence for an operculum in the cyclomyans, but simply because the muscle pads appear to be homologous with the cephalic muscles in tergomyans, archinacelloideans, and modern limpet gastropods. If the cyclomyans were exogastric, like the tergomyans, the cephalic muscles of these animals then would have been attached to the back of the shell above the visceral hump and well away from the head, which makes no sense. The head must have been situated below the cephalic muscles and on the opposite end of the body whorl from the coil, indicating the cyclomyans were endogastric. While this is not an impossible situation in monoplacophorans, in view of most efficient muscle function a more likely explanation is that the cyclomyans were gastropods.

We envision a complete range of shell muscles arranged in a functional sequence (Fig. 4) based on coiling parameters and apertural characters, which in turn were very probably based on mode of life and physical environment. According to figure 4, the uncoiled cyclomyans like *Cyrtonella* Hall were the most limpet-like forms, grading (functionally, but not necessarily phylogenetically) through the cyrtolitiform (e. g. *Cyrtolites* Conrad) and sinuitiform (e. g. *Sinuitopsis* Perner which has an anal emargination like the pleurotomarioideans) cyclomyans to the bellerophontoideans (e. g. *Bellerophon* Montfort). Forms such as *Sinuites* Koken, *Syvestrosphaera* Peel, and *Carcassonella* Horný and Peel were intermediaries, retaining the cephalic muscles of the limpets while accomplish-

ing retraction through application of lateral retractor muscles similar to the helically-coiled gastropods. These forms may have had a completely different mode of life from both the limpets and bellerophontoideans. In fact, Horný (1996) has described *Sinuites* Koken as a semi-infaunal gastropod based on secondary shell layers similar to those in the bellerophontoidean *Euphemites* Warthin (see Harper and Rollins, 1985). Pronounced variation in shell muscle position and pattern correlated with degree of shell coiling is also recognized in the Paleozoic platyceratids (Rollins and Brezinski, 1988).

PARIETAL DEPOSITS

Harper and Rollins (1982) and Wahlman (1992) were convinced that the most reliable criterion for assignment of any isostrophically-coiled mollusc to the Gastropoda was the presence of a massively developed parietal deposit. Such deposits are most easily viewed as functionally enhancing shell stability by placing the bulk of shell weight over the posterior foot, and less reasonable if elevated over the head of the animal. Rollins (1966) noted that the parietal pad of the bellerophont *Ptomatis* also displayed a central cleft that most likely rested directly upon the foot. Massive parietal deposits, however, are variously developed in bellerophonts. When present, they appear to confirm torsion and justify ready assignment to the Gastropoda. Their absence, or even the presence of a thin inductural wash, is inconclusive. As noted by Pojeta and Runnegar (1976), thin secondary shell deposits might have been secreted by epithelial tissue near the head of the animal.

DISCUSSION

It has become obvious that the monoplacophorans, at least those represented by *Neopilina* Lemche, do not represent the molluscan archetype (hypothetical ancestral mollusc). All of those forms we know or suspect to be monoplacophorans are too highly specialized, with their serial pairs of organs and muscles, the mantle covering the entire animal, and a pallial groove that completely encircles the body substituting for a centralized mantle cavity. However, given the close anatomical relationship of monoplacophorans and polyplacophorans, this must be the plesiomorphic condition from which the gastropods arose. Haszprunar (1988b) suggested that a shallow mantle cavity, with a concomitant degree of respiration in the mantle roof and margin, is the primitive condition in gastropods. In addition, Haszprunar believes the subpallial cavity was probably used for respiration until the gastropods evolved
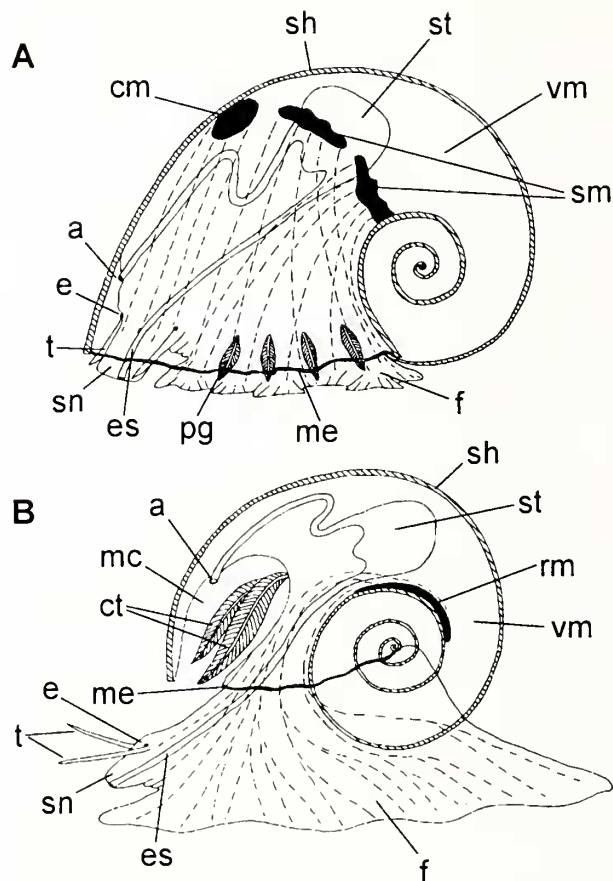

Fig. 3. Proposed configurations of head, foot, visceral mass, and various organs for: **A** - *Cyrtolites*, a representative cyclomyan; and **B** - *Bellerophon*, a representative bellerophontoidean. a - anus; cm - cephalic muscle; ct - ctenidia; e - eye; es - esophagus; f - foot; mc - mantle cavity; me - mantle edge; pg - pallial gill; rm - retractor muscle; sh - shell; sm - shell muscles; sn - snout; st - stomach; t - tentacle; vm - visceral mass.

secondary gills. The fossil record suggests otherwise, as shown below.

If, in fact, the fossil record is good enough, we should be able to see many of the morphological changes that evolved throughout the Phanerozoic in the tergomyans, cyclomyans, and bellerophontoideans. And indeed, we can. In figure 4 we show a series of hypothetical monoplacophoran and gastropod forms that are simply generalized models based on actual fossils such as *Tryblidium* Lindström, *Cyrtolites* Conrad, and *Bellerophon* Montfort. We envision a series of anatomical changes that occurred relatively rapidly in geologic time. Following torsion (Fig. 4, fundamental change A) the archetypal gastropod was a torted monoplacophoran having serially arranged muscles and organs, including multiple gills in a pallial groove surrounding the body. At some later time the population of archetypal gastropods gave rise to forms that increased the
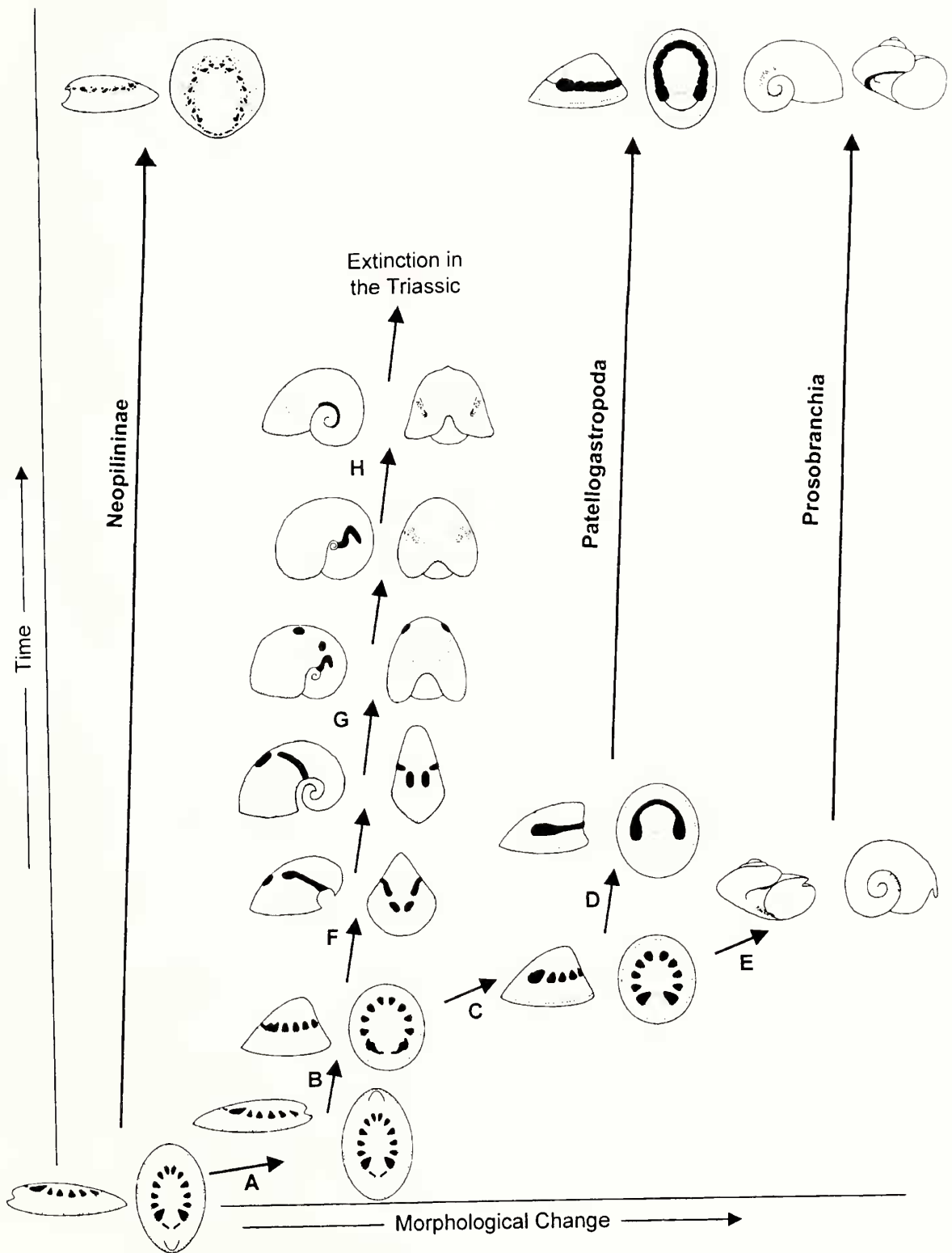
Fig. 4. Diagram illustrating a hypothetical generalized evolutionary scheme for the gastropods and monoplacophorans. Muscle scars are shown in black, stippled where hidden behind shell. Dotted lines indicate proposed extent of the mantle/pallial cavity. Letters designate fundamental changes in anatomy. **A** - torsion; **B** - vertical expansion of the shell; **C** - development of an anterior mantle cavity; **D** - decrease in afferent vessels, resulting in fusion of the muscles to a horseshoe; **E** - helical coiling; **F** - isostrophic coiling; **G** - development of an anterior mantle cavity; and **H** - reduction of shell muscles to two retractors.

height of the shell (B), allowing for enlargement of the pallial groove. Certain of these high-domed gastropods experimented with centralizing the mantle cavity and reducing the number of gills (C). This allowed a decrease in the number of afferent vessels and a consolidation of the discrete shell muscles into a horseshoe (D). These gastropods eventually gave rise to the Patellogastropoda, which are distinct from all other archaeogastropods (see Lindberg, 1988 for a review of this gastropod order). Whether or not there was a coiled intermediate in this lineage, as some authors have suggested, is beyond the scope of this discussion.

High doming and centralization of the mantle cavity also allowed a separate lineage to experiment with coiling, particularly helical coiling. These forms gave rise to the most successful group of molluscs, the prosobranchs.

Meanwhile, the original group of high-domed archetypal gastropods also were "experimenting" with coiling, probably as a means to increase the amount of visceral mass without making the shell unstable and/or to afford greater protection of soft organs within the shell, perhaps concomitant with a more motile existence. These gastropods, which we have been calling cyclomyans, retained the plesiomorphic pallial groove and multiple gills of the ancestral gastropods. Through time these molluscs enlarged the pallial groove and concomitantly moved the shell muscles farther back into the shell. This provided a morphological setting that would lead, eventually, to the independent development of the centralized mantle cavity. Once this important feature was attained, the cyclomyans went through an adaptive radiation that resulted in an explosion of forms within the morphospace of the isostrophically-coiled shell. This radiation, linked to probable predation pressures and adaptive changes to the physical environment, forced modification in the shell from evolute, open-coiled, limpets to tightly involute, compact animals that spread out into a variety of adaptive niches - the Bellerophontoidea. Unfortunately, as successful as they were, the bellerophont lineage decreased substantially in diversity toward the end of the Paleozoic and ultimately became extinct, but well into the Triassic, not at the biotic crisis of the Permian extinction.

SUMMARY AND CONCLUSIONS

During the 1970s and early 1980s, a controversy concerning the systematic placement of the Bellerophontoidea ("bellerophonts") – a group of planispirally coiled marine molluscs known only from the fossil record and commonly considered to be primitive gastropods - emerged in the paleontologic literature. Although some points of contention had been raised as early as the 1940s, the primary concern now focused upon interpretation of multiple, symmetrical muscle scars preserved on internal molds (steinkerns) of certain Bellerophontoidea. One camp insisted that, because multiple, symmetrical muscles suggest metamery, the Bellerophontoidea must have been untorted and, therefore, were monoplacophorans rather than gastropods. Another group insisted that "bellerophonts" were gastropods. Yet a third camp argued that single pairs of muscles and various gastropod-like features of some "bellerophonts" indicate that many of these animals were gastropods. They conceded that other Bellerophontoidea were monoplacophorans and, although distinguishing between the separate lineages would be difficult, it could be done by analyzing all the shell features and not just the muscle scars (which were notoriously rare). In 1982 we presented evidence that the various arguments for "bellerophonts-as-monoplacophorans" were specious and concluded that all "bellerophonts" were gastropods. A reexamination of that evidence and consideration of research on these molluscs since 1982 has failed to convince us otherwise.

Following torsion, the archetypal gastropod was a torted monoplacophoran having serially arranged muscles and organs, including multiple gills in a pallial groove surrounding the body. At some later time the population of archetypal gastropods gave rise to forms that increased the height of the shell, allowing for enlargement of the pallial groove and centralization of the mantle cavity, and eventual development of the Patellogastropoda. High doming and centralization of the mantle cavity also allowed a separate lineage to experiment with helical coiling leading to the very successful Prosobranchia. The original group of high-domed archetypal gastropods also "experimented" with coiling, and this group, which we have been calling cyclomyans, retained the plesiomorphic pallial groove and multiple gills of the ancestral gastropods. This provided a morphological setting that would lead, eventually, to the independent development of the centralized mantle cavity and the adaptive radiation of the Bellerophontoidea.

The evolutionary scenario we described is speculative, of course, but it does have its basis in the fossil record and in comparative anatomy. We conclude, as we did previously (Harper and Rollins, 1982), that the Cyclomya and Bellerophontoidea were gastropods rather than monoplacophorans, and Cyclomya should be retained as a suborder of Bellerophontina. Only the Tergomya were, and are, true monoplacophorans.

It should be apparent that there is no reason to abandon the term Monoplacophora. Even though it originated as an informal name, and recently became a "garbage can" term for an unlikely grouping of exotic molluscs and, perhaps, non-molluscs, Monoplacophora should be retained as a formal class name. The taxonomic scope of this term has come full circle - originally proposed to include only

the Tryblidiidae, it once again can be defined as the Tryblidiidae and associated Recent neopilinids. The term Tergomya then is synonymous with Monoplacophora and should be abandoned. Cyclomya should be retained as a suborder of Bellerophontina.

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